XXIX.—*Report on a memoir by* M. P. Duchartre, *entitled 'Observations on the Organogeny of the Flower of the* Malvaceæ.' By MM. Brongniart, Richard and De Jussieu*.

We have been requested by the Academy to give an account of the botanical memoir presented by M. Duchartre, and bearing the above title.

M. Duchartre has distinguished himself by various investigations, several of which have had the same object as the present, but related to different plants; many of them have been submitted to the Academy and have received its approbation. These researches may serve to explain several particular questions relating to the vegetables to which they refer; but in addition to their interest in this point of view, they are of much greater importance for the solution of general questions. We shall commence by giving a sketch of them, and enunciating the problems to which they relate, before detailing the results at which the author has arrived in seeking for their solution.

It is well known that botanists agree pretty generally in considering that the different parts of a flower represent so many more or less modified leaves. These leaves, which constitute the segments of the calyx and of the corolla, the stamens and the parts of the pistil, are sometimes independent of each other as the true leaves generally are, sometimes coherent by a portion of their margins or their surfaces. DeCandolle, who has contributed so much to the establishment of this theory, has proposed the word *soudure* (confluence) to express this union, which implies that the parts were primarily separate before being thus combined. However, he admitted that the separation could only have existed prior to that period at which the parts become accessible to observation, and then this adhesion is called by him *predisposed*. But that which he had not been able directly to establish, others might anticipate doing, when the perfection of instruments and methods of observation had removed the barrier by which he was checked. This is, in fact, what has been accomplished. With the aid of the microscope, the development of the organs has been traced from their first appearance; that is to say, from the moment at which they separate from the axis to which they are attached, and appear constituted simply by the aggregation of a few cells.

Now, are these primary rudiments constantly or only occasionally independent of each other? Upon this point observers are not agreed.

M. Schleiden speaks decidedly for the primitive independence

* Translated from the Comptes Rendus for August 15, 1845.

of the parts*: "In all those calyces and corollæ called *monophyllous*, the various parts, which subsequently cohere, are at their origin everywhere, and without exception, separate, and their independent existence is prolonged for a sufficient length of time to render all reasoning on the number of parts superfluous, because it is a matter of observation susceptible of demonstrative evidence." He subsequently maintains the same original independence of the stamens and carpels. He has supported his conclusions by numerous examples, and especially, at a later period, by a very detailed history of the development of the flower of one of the papilionaceous *Leguminosæ*.

However, on the other hand, M. Adolphe Brongniart † had established the fact, that in the very young buds of monopetalous flowers, the corolla at first forms a kind of minute ring around the stamens. A high authority, Mr. R. Brown ‡, also adopts this view: he says, "In the description of the modifications of the ovary and stigma which I have given, in conformity with the ordinary language of botanists, I have employed the term *confluence*, by which however we must not understand the union or cohesion of parts originally distinct. For in the great majority of cases, the separation or the complete development of these parts from their original cellular and pulpy state has never occurred; but with this understanding the term may be preserved, unless we prefer the word *connate* as subject to less objection." The previous memoirs of M. Duchartre led to the same result, by proving in certain cases the union of certain parts of the flower after their first appearance; and we shall see that he has found new examples of this original cohesion in the *Malvaceæ*.

There is another class of facts in the history of the flower which may throw great light upon organogenic researches; such are those known by the name of *duplication*. Frequently in the place which should be occupied by a single organ we find two or more arranged in the same plane, or in several different planes, *i. e.* in bundles. Each of these bundles may then be considered to represent a single leaf. Is this the case? and how has this multiplication of organs, this duplication of a single one, occurred?

The family of the *Malvaceæ* is well-chosen for studying this question. In that of the *Byttneriaceæ*, which was once united with it, and which, although now separated, cannot be far removed from it, and evidently forms part of the same natural group, we sometimes find only five stamens opposed to as many petals; sometimes opposite each petal, a system of several united

* Wiegmann's Archiv. [A translation of this paper appeared in the Philosophical Magazine for Feb. 1838. Ed.]

† Ann. des Sc. Nat. vol. xxiii. p. 229. ‡ Plant. Javan. Rar. p. 112.

stamens, consequently represented in the first case by a single one; and alternating with these systems of stamens in a circle a little more internally situated, an equal number of lobes or teeth, which according to the laws of position should represent the row of normal stamens,—that which should alternate with these same petals. In the true *Malvaceæ* we find a large number of stamens cohering inferiorly into a single hollow column, which envelopes the pistil; but notwithstanding the apparent confusion resulting from their multiplicity, it is not difficult to perceive, in many cases, that this collection of stamens is divided into five groups, which are opposite to the petals; and even where it is difficult to prove this distinction, it is indicated by the existence of double vascular bundles, which, arising from the base of the petal, follow the column to its summit, where it divides into a large number of antheriferous filaments. Frequently the column within and above these threads is divided at the summit into five more internal teeth alternating with these vascular bundles, and these more or less distinct groups of stamens; these teeth are incontestably analogous to those described in many of the *Byttneriaceæ*. Finally, in the centre of the flower we find a pistil composed of five more or less intimately combined carpels; but at other times the carpels are more than five, and even become very numerous, and either still arranged in a circle or situated at unequal heights, so as to form together a kind of capitulum. Does each of these carpels then represent a carpellary leaf? or is each of these five carpellary leaves doubled so as to simulate several? Their arrangement in five distinct systems can hardly leave a doubt on this point in *Kitaibelia*; but in *Malope*, and others of the same group, an apparent confusion results from the unequal or completely arrested developments of a certain number of carpels.

In tracing these parts from their first appearance, we should expect a decided answer to these questions; this is what M. Duchartre has proposed in the memoir before us, and which it remains for us to analyse.

The calyx, which at a later period becomes monophyllous with five divisions, appears at first in the form of a continuous rim, surrounding the central mass of the flower, bounded by a large convex tubercle having no distinction of parts. This border soon sends off five small festoons, which correspond to the five sepals thus united at the base from the commencement. The author insists upon this mode of formation, which he has found in the envelopes of all those flowers having a monophyllous calyx or corolla, the development of which he has had an opportunity of studying. The petals and stamens may be subsequently distinguished and are simultaneously developed, so that it is well to

trace their evolutions together. Soon after the appearance of the calyx, the margin of the central tubercle becomes raised into five smaller tubercles, which are rounded, alternating with the segments of the calyx, and thus representing the floral whorl which immediately succeeds it. Each of these tubercles soon appears like two in juxtaposition, its development ensuing more rapidly at the two sides than in the median line; and thus, instead of five small primitive eminences, we have five pairs. Nearly at the same time a slight transverse fold appears below and outside of each of these five projections; this appears to be another appendage of the tubercle, which, at first single, subsequently becomes double. The fold becomes the petal; the tubercles become stamens. Hence the petals and stamens here belong to one and the same group of organs developed from a base which is common to that spot which in most flowers is occupied by the petal alone.

The petal in its further development, which is generally rather slow, much more so than that of the stamens, does not become doubled, and gives no other indication of this tendency except in its more or less bilobate summit.

Not so however with the stamens; for shortly after the first ten staminal tubercles have become distinct, we find that a formation perfectly similar to the first is produced. Five new pairs of tubercles opposite to the first appear in a more internal circle; then a third arranged concentrically, and consisting of ten other tubercles; then a fourth, so that the total number is successively doubled, tripled, and quadrupled. We thus have ten radiant series, opposed in pairs to the petals, and supported upon a common base, which is frequently cut into five corresponding lobes, more or less marked. At a little later period, each of these tubercles, continuing to grow more at the sides than in the median line, is itself divided into two, and we find that four parallel series become substituted for the two before each petal, and the total number is a second time doubled. The same occurs in those flowers which have very numerous stamens; but there is a slight difference in those in which they exist in less numbers. Then, either fewer concentric rows are formed, or each of these rows stops at that period at which the pairs are simple and not doubled, or within the first pairs a single tubercle only is formed; this is slightly lateral and oblique, then another still more internal and on the opposite side, so that within the first pair we find only isolated tubercles, sent off alternately, first from one side, then from the other, in a zigzag direction. In all cases, there are invariably five systems of stamens opposite to the petals.

During these changes, the small common tube, to which all these organs are attached, continues to elongate, raising these

concentric formations so as to produce a system of stages arranged one above the other; and although they enlarge at the same time, they do not do so in the same proportion. The organs which enlarge do not then find sufficient room to lie side by side in regular and concentric circles; they become rather confusedly mixed, and the original symmetry becomes less and less apparent. When they have arrived at a certain degree of development, each of the tubercles shrinks up at the base into a minute filament which becomes more and more elongated. Each also becomes marked by a median furrow, and buried within two cells which subsequently fuse into a single one. In short, these are so many reniform, unilocular anthers, which tend more and more to assume their definite form.

In several species M. Duchartre has observed an ulterior change, from which a new increase in the number of stamens results. Several of them are curved into a horse-shoe form, and terminate by becoming divided into two by a constriction of the summit of their curve,—a constriction which ends by forming a complete solution of continuity; this, extending from above downwards, also divides the filament which was at first simple into two corresponding to the anthers thus formed. This is a true duplication.

This term would apply with less accuracy to the anterior formations, from which the multiplication of the stamens has resulted; for we may say, that at each of these changes they have doubled rather than multipled. Be this as it may, we have clearly five groups of organs alternating with the five leaflets of the calyx, each comprising a petal and several stamens, supported upon a base which is common and simultaneously developed. This is the whorl which is within and alternate to the calyx, and which is ordinarily called the corolla, with this difference, that here each petal is replaced by a group or bundle of organs.

One of us has long since professed the doctrine, that in those flowers which have stamens double in number to the petals, whenever the stamens of the external row are opposed to the petals (and this is most frequently the case) they do not constitute a distinct whorl, but form a part of that of the corolla. The development of the flower of the *Malvaceæ* supports this opinion, exhibiting to us each of the petals, opposed, not to a stamen, but to an entire bundle. We may add, that such appears to be the most common symmetry in polyadelphous polypetalous flowers, as is seen in so many *Myrtaceæ, Hypericaceæ,* &c., where the bundles, which are perfectly distinct, are opposite to the petals.

But what has become of the normal whorl of the stamens,—that which should alternate with the petals? M. Duchartre discovers this in the five terminal lobes of the staminal tube, situated upon

a plane anterior to that of the filaments, alternating with their five groups,—lobes which we observe in many of the *Malvaceæ*, although they are barely perceptible, and even are entirely wanting in many others. MM. Dunal and Moquin-Tandon recognised them, and considered them as the border of a five-lobed disc. But the nature of the disc is far from rigorously defined, and in many cases this term exactly applies to abortive whorls, as may be seen in many *Viniferæ*, in the *Myrsineæ*, &c.,—families which are equally remarkable by the opposition of their stamens to the petals, to which they are equal in number. M. Duchartre mentions this example of the *Myrsineæ* as exhibiting exactly the symmetry of the *Malvaceæ*, with this difference, that a single stamen only corresponds to each petal. We do not agree with him in this opinion, but think that in the *Myrsineæ* there are two whorls of stamens independent of the corolla, the external or that alternating with the petal being metamorphosed or abortive. This appears to be demonstrated by the flowers of *Theophrasta*, or better still by *Jacquinia*.

The author, arriving at the pistil of the *Malvaceæ*, finds in their different genera variations which are sufficiently considerable to establish four different categories, which he successively examines. In the first the quinary symmetry is at once apparent, and the five carpels differ but little in their mode of development from the views and theories generally adopted. In fact, we know that each carpel is considered as a leaf folded on itself, and that numerous organogenic observations exhibit this organ to us in the form of a minute scale which soon becomes concave internally, then tends more and more to close up by the approximation of the borders of the concavity, the adhesion of which completes the formation of the ovary and forms a perfectly closed cavity, in which one or more ovules subsequently become developed. Now, imagine five of these scales or plates soldered together by their lateral surfaces, we then have the first condition of the pistil of *Hibiscus*. That will be a small border having five angles, which alternately project and recede internally; the projecting angles correspond to the borders of five carpels, approximated in pairs, and these angles projecting more and more and converging, terminate by uniting so as to form a quinquelocular ovary. But at a still earlier period, before the internal projections were marked, we had a pentagonal border which soon becomes festooned by five tubercles, the first indications of the styles.

In a second category, *Malope* for instance, we also observe a pentagonal border, the five angles of which are opposite to the petals, and consequently correspond to the place which five normal carpels should occupy. That border of the pentagon which is first united sends out a series of rounded tubercles, which sub-

sequently become slightly swollen externally and inferiorly, so that each tubercle presents two enlargements; one external and inferior, the future ovary,—another superior and internal, the future style. The latter becomes elongated and raised in proportion as the former increases in size; but as it elongates, the stylous portions, remaining distinct at their summits, are confounded at their base, —at least all those which correspond to the same angle of the common support of the carpels; an angle which becomes more and more marked as far as the point at which the entire body is as it were cut into five oblique lobes loaded with ovules on every part of their surface. A bundle of styles, equal in number, distinct superiorly and united inferiorly, thus corresponds to each of these systems of ovaries; and each of these systems, in the general symmetry, plays an analogous part to that which we have found assigned to each of the bundles of stamens, because it occupies the place which a single carpel should occupy, and which it consequently represents. How is the cavity of the ovary formed?

M. Duchartre has not in this case found that the margins of a folded leaflet approximate towards one another, then touch and adhere; but, at a certain period, dissection has exhibited to him the cellular mass of the ovary excavated by a slight fissure, which continues to enlarge, without any manifest external appearance.

A third category, and that includes the greater part of the *Malvaceæ*, exhibits the carpels not in constant relation with the quinary number of the other parts of the flower; but they form a perfect circle, are not grouped into five systems, and frequently their entire number is no multiple of five. However, M. Duchartre is led to believe that the same symmetry occurs here as in the preceding case. The ovaries and styles are developed in the same manner, with this difference, that all the styles are united inferiorly into a single cylinder.

Finally, a fourth category seems to belong to the first by the quinary number of the carpels; but here we observe ten tubercles on the pistillary border, which subsequently form ten summits of distinct styles, and which correspond in pairs to five ovaries, the centre of which also becomes hollowed by a fissure, which forms its cavity without any change being externally apparent.

The necessary conclusion from all these observations is, that the parts, from their earliest appearance, present the relations of adhesion which they subsequently exhibit in the perfect flower. The monophyllous calyx on its first appearance was a body simple at the base. The petals, coherent by their base with the staminal tube, originated from a base common to them with the stamens, and the latter at their origin were united by this base in the same

manner as they appear subsequently. The ovaries were from the first grouped and adherent together, nearly in the same manner as the flower subsequently exhibits them, their styles being distinct at the summit, coherent in the rest of their extent, which has been more slowly developed. As regards the peculiar results to be deduced from these observations relative to the symmetry of the flower of the *Malvaceæ*, we have noticed them above, and it would be useless to repeat them.

Undoubtedly we have not been able ourselves to verify all these facts, for this would occupy almost as much time as that devoted by the author to the original investigations; but we have verified a sufficient number to justify the truth of most of them. We regret that M. Duchartre has not carried out his extensive researches still further, so as to teach us by anatomical details the formation of the tissues in the organs, the external forms of which he describes, and informing us at what periods the developments he describes correspond to the changes gradually established in the tissues, which are at first entirely cellular.

We think that these details would throw a new light upon the phænomena of duplication, which are still so obscure, and would enable us better to comprehend the mechanism of this substitution of several fascicled organs for a single plane organ. The formation of cavities by an excavation in the centre of a cellular mass, which assimilates certain carpels closely to anthers, is a fact so much opposed to the generally admitted theories as to require new observations and more development, especially by connecting with it the history of the ovule, and ascertaining how it is formed in the cavities thus produced.

We acknowledge that these are researches of extreme delicacy, since the point at which M. Duchartre has arrived presented incontestable difficulties, and the dissection of such minute bodies is exceedingly tedious, and even sometimes appears impossible. But for some years we have seen that microscopic observation surmounts difficulties which had long been considered insurmountable, and facts, the direct knowledge of which had been despaired of, have become familiar to all those who are occupied in this kind of researches: just as those parts of the earth which were long unknown, now, being frequented, have become easily accessible, and from them we set out for more remote unexplored parts. These reflections must not be looked upon as detracting from M. Duchartre's investigations, but rather as an encouragement for pursuing them. We address them to him the less reluctantly, because what he has already done proves what he is capable of doing.